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Plant diversity patterns in the Aljibe Mountains (S. Spain): a comprehensive account

F. OJEDA[1], T. MARAÑÓN[2,*] and J. ARROYO[1]
*[1]Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Apartado 1095; [2]IRNA, CSIC, P.O. Box 1052, 41080 Sevilla, Spain; *Author for correspondence (e-mail: teodoro@irnase.csic.es; fax: +34-95-4624002)*

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Abstract. The Aljibe Mountains are located in the southern tip of the Iberian Peninsula and have a remarkable biogeographical interest. The complete plant species list (trees, climbers, shrubs, perennial and annual herbs, ferns, lichens, bryophytes and macroscopic algae) was recorded in four 0.1 ha plots from each of the most representative community types (*Quercus suber* woodland, *Q. canariensis* forest, open heathland and *Q. coccifera* shrubland). Up to 119 plant species were found in total in the *Q. suber* woodland plot. The diversity of woody plants was analysed from 44 samples of cover (100 m line), and the herbaceous layer was explored in 200 quadrats (of 0.5×0.5 m). Three biodiversity components (species richness, endemism, and taxonomic singularity) were evaluated in both shrub and herbaceous layers. Open heathlands showed the highest richness of endemic species, both woody and herbaceous. The highest number of woody species was found in the evergreen *Q. suber* woodland, and of herbaceous species in the semi-deciduous *Q. canariensis* woodland. Taxonomic singularity was higher in *Q. canariensis* woodlands and *Q. coccifera* shrublands for woody species, but there were no significant differences in the herbaceous layer. Local species diversity of heathlands in this region resembles that of South African heathlands (fynbos), despite the obvious geographic and floristic distance, and contrasts with the low diversity of biogeographically closer, European temperate heathlands. The Aljibe Mountains show high diversity values for different life forms (from trees to mosses) and spatial scales (from community to region), and are rich in endemic species. Thus, this area should be recognised as a relevant unit within the Mediterranean plant diversity hot spots.

Key words: biodiversity, endemism, Gibraltar, life-form, Mediterranean vegetation

Introduction

Geographical areas containing high species richness, high levels of endemism, and/or harbouring a high number of rare or threatened species, have been defined as biodiversity hotspots, and have been considered to set priorities for conservation planning (Myers 1988, 1990; Reid 1998). Ten hotspots for plant diversity have been proposed within the Mediterranean Basin (Médail and Quézel 1997), one of them being the Baetic–Rifan complex, in southern Spain and northern Morocco (Figure 1). High species richness and endemism characterise this region. Isolation through altitude in high mountains and, to a lesser extent, through edaphic differentiation by soil types derived from serpentine, gypsum, limestone or dolomite substrates, account for most plant endemism in this region (WWF and IUCN 1994; Médail and Quézel 1997).

The area surrounding the Strait of Gibraltar, in the western end of the Baetic-Rifan region (Figure 1), includes acidic, nutrient-poor, siliceous sandstone-derived soils (Ojeda et al. 1996), otherwise scarce within the Mediterranean Basin. A mild Mediterranean climate, due to oceanic influences, also characterises this region (WWF and IUCN 1994). Both ecological features, together with its particular history, seem to have promoted plant diversification, singularity and endemism in this area (Arroyo 1997), and favoured the persistence of an extensive woodland landscape (Marañón and Ojeda 1998).

Previous studies (Arroyo and Marañón 1990; Ojeda et al. 1995, 1996; Marañón et al. 1999) have highlighted the high diversity levels of woody plant communities of

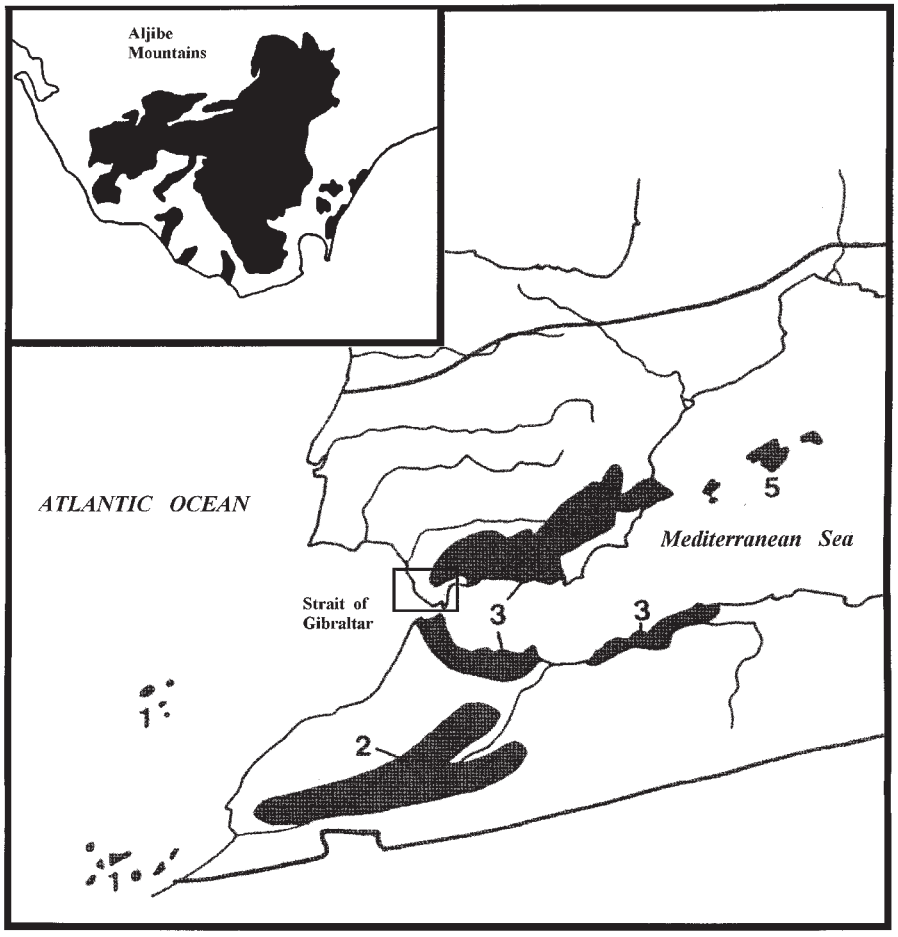

Figure 1. Map of the plant biodiversity hot-spots within the West Mediterranean Basin (after Médail and Quézel 1997). The Baetic-Rifan complex is marked with number 3 (other numbered hot-spots are: Canarian and Madeiran archipelagos, no. 1; High and Middle Atlas Mountains, no. 2; and Thyrrenian islands, no. 5). Insert illustrates the Oligo-Miocene sandstone formation (after Didon et al. 1973) which have formed the Aljibe Mountains in southern Spain.

the Strait of Gibraltar region. This area has also been frequently visited by botanists, mainly interested in the occurrence of temperate and Macaronesian disjunct relict species. However, it has been overlooked in most global and regional biodiversity assessments (e.g. WWF and IUCN 1994; Heywood and Watson 1995; Médail and Quézel 1997; Webb 1998; but see Castro et al. 1996).

In spite of the biogeographical and botanical interest of this area, a complete modern flora (or at least a checklist giving a precise account of its extant plant taxa) is still lacking. The northern side of the Strait of Gibraltar (Figure 1) is covered by the regional flora of Western Andalusia (Valdés et al. 1987), and by the more general floras of the Iberian Peninsula (Castroviejo et al. 1986–1999, still incomplete) and of Europe (Tutin et al. 1964–1980). Both the European and African sides are included in the general checklist for the countries in the Mediterranean Basin (Greuter et al. 1984–1989, still incomplete).

A complete list of the plant taxa of this region or a standard flora is therefore essential, but not sufficient to adequately evaluate its biodiversity. Ideally, this complex, integrated parameter should encompass the variability at the genetic level (genotypes of individuals and genetic structure of populations), at the species level (species richness, endemic species, phylogenetic singularity, ecological function) and at the community and regional levels (spatio-temporal dynamics of vegetation mosaics in the landscape) (Gaston 1996). We have acknowledged this multilevel approach in the study of plant diversity (Arroyo 1997) and have carried out some preliminary analyses of biodiversity components (species richness, endemic richness and taxonomic singularity) of woody plant communities in woodlands, heathlands and shrublands in both sides of the Strait of Gibraltar (Ojeda et al. 1995, 1996; Marañón et al. 1999).

In this paper, we focus on the Aljibe Mountains area, at the northern (European) side of the Strait of Gibraltar, within the Baetic-Rifan region (Figure 1). The relatively well-known flora and the previous studies on woody plant community diversity, make this region suitable as a study-case to quantify its biodiversity at different approaches and spatial levels. We have first monitored the complete list of plant species (trees, climbers, shrubs, perennial and annual herbs, ferns, bryophytes, lichens and macroscopic algae) in four 0.1 ha plots, representing the main vegetation types in this area, and have compared them with analogous existing data for the Mediterranean-type regions (Westman 1988).

We have also quantified species richness, endemism and taxonomic singularity, separately for the shrub and the herbaceous layers, as components of their biodiversity (following Ojeda et al. 1995), and have made subsequent between-community comparisons for these three diversity parameters.

Finally, we have analysed the species-area relationship of the region including the study area (Andalusia, southern Spain), and have compared them with data from the Cape Floristic Region, the Mediterranean-type area with highest diversity values and a physiognomically similar vegetation type to that in the study area (i.e., heathland; Cowling et al. 1992).

The main goal of this study is, not only to describe the patterns and quantifying the levels of plant biodiversity in the Aljibe Mountains, but also compare them with existing data from other Mediterranean-type areas in order to highlight the biodiversity value of this area.

Methods

The study area

The Aljibe Mountains are located at the southern tip of the Iberian Peninsula, on the northern side of the Strait of Gibraltar (Figure 1). The rough topography, with highest elevation of 1092 m, is mainly composed of Oligo-Miocene sandstone, which produces acidic, sandy, nutrient-poor soils. Limestone outcrops, which produce limy, basic soils, are also found, although scattered and much less abundant. In the lowlands fringing the mountains, non-acid, loamy or marly soils are dominant (CEBAC-CSIC 1963; Didon et al. 1973).

The climate is Mediterranean-type with cool, humid winters and warm, dry summers. The total annual rainfall ranges from 665 mm in the lowlands to 1210 mm in the mountains. Mean temperature is mild, 16–18 °C, with monthly maximum of 31 °C and monthly minimum of 5 °C (Ojeda 1995). In summer, these mountains intercept moist, SE-prevailing winds coming directly from the Mediterranean Sea, which reduce to some extent the severity of drought.

The evergreen tree *Q. suber* (cork oak) dominates most woodlands in this area, whereas semi-deciduous *Q. canariensis* is a locally abundant tree in valley bottoms. *Quercus pyrenaica*, another semi-deciduous oak tree, forms small, dense patches at higher altitudes, over 900 m. Riparian forests are more diverse in the tree and arborescent shrub overstorey, harbouring temperate-climate tree species such as the deciduous *Alnus glutinosa*, *Fraxinus angustifolia*, *Frangula alnus* (distinguished here as the subsp. *baetica*), and the evergreen *Ilex aquifolium* and *Laurus nobilis*. The sandstone ridges and hilltops are covered by open heathlands dominated by *Erica australis*, *Cistus populifolius* subsp. *major* and *Genista tridentata*, among other species. Limestone outcrops, and marly and loamy lowlands are dominated by garrigue-type shrublands, where robust, sclerophyllous shrub species such as *Q. coccifera*, *Pistacia lentiscus*, *Olea europaea* and *Myrtus communis* become dominant.

This area was protected in 1989 as *Los Alcornocales* Natural Park, covering 1700 km^2, aimed to promote the sustainable management of forest resources and to maintain its biodiversity (JA 1997). Main resources are cork extraction from *Q. suber* trees, (their bark is stripped off every 9 years), free-range livestock (mainly cattle), game hunting (red- and roe-deer), and, more recently, eco-tourism (Blanco et al. 1991; Ibarra 1993; Marañón and Ojeda 1998).

Plant inventories, sampling and data analysis

In a previous study (Ojeda et al. 1995), we distinguished four main types of woody plant communities (excluding riparian forests): (i) dominant *Q. suber* woodland on middle slopes; (ii) *Q. canariensis* forests on valley bottoms; (iii) open heathlands on ridges; and (iv) sclerophyllous *Q. coccifera* shrublands on marly lowlands and limestone outcrops. We set a permanent 20 × 50 m plot in each community type. Linear cover of woody species from both overstorey tree and understorey shrub layers was measured along the two 50 m plot lines. Two sets of 25 quadrats of 0.5 × 0.5 m were also established along the same lines and examined on a monthly basis (from December 1992 to December 1993), so as to record the presence of herbaceous species. In addition, each 0.1 ha plot was explored for new records of woody and non-woody angiosperm species and, specifically, to list lichens, bryophytes and macroscopic algae present in the plot. The non-vascular species are seldom considered in plant diversity databases, mainly due to practical constraints, but they should be included in any complete plant diversity account since they may have ecological interactions with vascular plant species. Taxonomic nomenclature follows Valdés et al. (1997) for vascular plants.

The four complete plant inventories at the 0.1 ha scale have been arranged according to their life forms. Total numbers of vascular species in these inventories have been compared with analogous data from other Mediterranean regions (Westman 1988) by means of a one-way ANOVA. Subsequent multiple post-hoc comparisons were made by HSD Tukey's tests for unequal sample sizes (StatSoft 1997).

The contribution of the main plant families to the 0.1 ha diversity was assessed separately for woody and non-woody species. The families Cistaceae, Ericaceae, Fabaceae and Lamiaceae were considered for the woody component, and Asteraceae, Fabaceae and Poaceae for the non-woody component. Percentages of species for each family, in the 0.1 ha plots, were compared with the proportion of the family diversity (either woody or non-woody) within the spermatophyte flora of the region (Valdés et al. 1987). Fern species were not considered here because of the very different taxonomic status of their families. Significance tests of differences between two percentages were used (StatSoft 1997).

The diversity of the shrub layer was analysed using 44 samples of 100 m line cover of woody plants. This data set was made grouping 31 samples from Ojeda (1995) and 13 samples from the Hozgarganta basin (northern part of the Aljibe Mountains; Garrido and Hidalgo 1998).

The relationship between environmental variables and species abundance was examined by CCA analysis using PC-ORD (McCune and Mefford 1997). Plant cover measures were logarithmically transformed. A set of eight environmental variables, including altitude, soil pH and fertility (P and K concentrations), incidence of fire, slash and browse, and overstorey tree cover, was correlated with the floristic matrix. The significance of the axis-environment relationships was tested by Monte Carlo

permutation test ($n = 99$ runs, McCune and Mefford 1997). Groups of samples were defined by cluster analysis using Sørensen distance and group average (UPGMA) linkage method (McCune and Mefford 1997).

Three biodiversity components were calculated for each plot (as in Ojeda et al. 1995): (i) species richness or number of woody species intercepted by the 100 m line; (ii) endemism level, considered as the number of species with geographic range restricted to Iberian-North African region or smaller enclosed areas; and (iii) taxonomic singularity, calculated as the inverse of the average of species number per genus for a given flora (in this case, the flora of Western Andalusia by Valdés et al. 1987). Endemism and taxonomic singularity were assessed for vascular species only, since this information is implicitly included in standard floras, which usually only consider vascular plants. Chorology and taxonomy of non-vascular species is far from comprehensively and homogeneously known. Shannon and equitability indices of diversity (Magurran 1987) were calculated using PC-ORD (McCune and Mefford 1997). Differences in the biodiversity parameters (species richness, endemic species richness and taxonomic singularity) and diversity indices between community types were tested using one-way ANOVA tests on rank-transformed data so as to avoid existing heterocedasticity problems (Conover and Iman 1981). Subsequent HSD Tukey's tests for unequal sample sizes were used when appropriate for multiple *post-hoc* comparisons (StatSoft 1997).

A combined matrix of 200 inventories of herbaceous species in 0.25 m^2 quadrats (50 quadrats $\times$ 4 plots) was analysed by DCA (Gauch 1992). Biodiversity components were calculated as for the shrub layer (see above). Between-community differences in all these biodiversity parameters were tested by means of one-way ANOVAs and subsequent multiple comparisons through HSD Tukey's tests (StatSoft 1997).

The species-area comparative analysis was carried out considering six nested areas for Andalusia and four nested areas for the Cape Floristic Region (see Table 6 for area sizes and their number of species). We have used linear regression procedures separately for each region and have subsequently compared both regression slopes using a test of parallelism (StatSoft 1997).

Results

Plant inventories at 0.1 ha scale

Environmental factors for the four 0.1 ha plots are shown in Table 1. Three sites are located on sandstone with acidic soils (pH 4.9–5.3) and one site on limestone (pH 6.0). Two sites are in woodlands (94 and 43% of tree cover), one in an open heathland and one in a garrigue-type shrubland.

A high number of vascular and non-vascular plant species (up to 119) were identified and counted in the two woodland sites. The more mesic *Q. canariensis* woodland

Table 1. Environmental features of the four 0.1 ha plots in the Aljibe Mountains.

Environmental variables	*Quercus canariensis* forest	*Quercus suber* woodland	Heathland	*Quercus coccifera* shrubland
Geology	Sandstone	Sandstone	Sandstone	Limestone
Altitude (m)	700	500	500	250
Annual rainfall (mm)	1209	970	970	665
Soil features				
pH	4.9	5.3	4.9	6.0
Organic carbon (%)	5.2	3.2	5.8	4.8
Potassium (%)	0.3	0.4	0.4	0.9
Calcium (%)	4.5	6.0	2.8	25.8
Phosphorus (%)	7.1	0.1	0.1	0.1
Iron (ppm)	165.0	48.5	50.8	22.3
Aluminium (ppm)	0.1	0.0	2.7	0.0
Overstorey tree cover (%)	94	43	18	4
Fire disturbance	Low	High	High	Low
Browsing disturbance	Low	Low	Low	High

had fewer species (91) than the drier, more open *Q. suber* woodland (119), in particular due to the lower number of shrub, and biennial/annual species, and despite the higher number of ferns (Table 2).

The heathland community also had a high number of species (85), but lacked the climber life form. The garrigue-type, *Q. coccifera* shrubland, had the lowest number of plant species (55) among the four sites, and was notably species-poor in bryophytes and lichens (Table 2). Non-vascular plant species contributed importantly (more than 20 species) to species richness of woodland and heathland on sandstone. Additionally,

Table 2. Number of plant species (including non-vascular) and life forms in four 0.1 ha plots.

Life-form	*Quercus canariensis* forest	*Quercus suber* woodland	Heathland	*Quercus coccifera* shrubland
Tree and arborescent shrub	6	6	4	6
Climber	3	2	0	1
Shrub	11	22	20	19
Geophyte	6	6	5	3
Perennial herb	33	32	24	16
Biennial and annual	8	27	11	7
Total flower plant species	67	95	64	52
Fern	5	1	1	0
Bryophyte	4	9	8	1
Lichen	15	14	12	2
Total plant species	91	119	85	55

one species of macroscopic alga, *Pleurococcus* sp. was found in the *Q. canariensis* forest (although it has not been included in Table 2).

Comparison with the Mediterranean data-base

We have represented the mean values of vascular species richness, at the scale of 0.1 ha, for the five Mediterranean regions in the world (Figure 2). Within the Mediterranean Basin, we have separated three subsets of data: North-west (France), East (Israel and Turkey), and South-west (Spain) Mediterranean sub-regions. Spanish samples (lacking in Westman's data base) are the four plots examined in this study and one plot of savanna-like *dehesa* (Marañón 1985).

The samples from California, Australia and north-western Mediterranean have the lower mean species richness (below 50 species/0.1 ha). Those from South Africa are intermediate (mean of 64 species/0.1 ha). The highest values correspond to eastern and south-western Mediterranean (mean above 80 species/0.1 ha). Chilean samples are very variables, and not significant differences were detected with other regions (Figure 2). However, this result must be considered as preliminary, due to the small sample size of some regions, such as Chile ($n = 4$), SW and NW Mediterranean

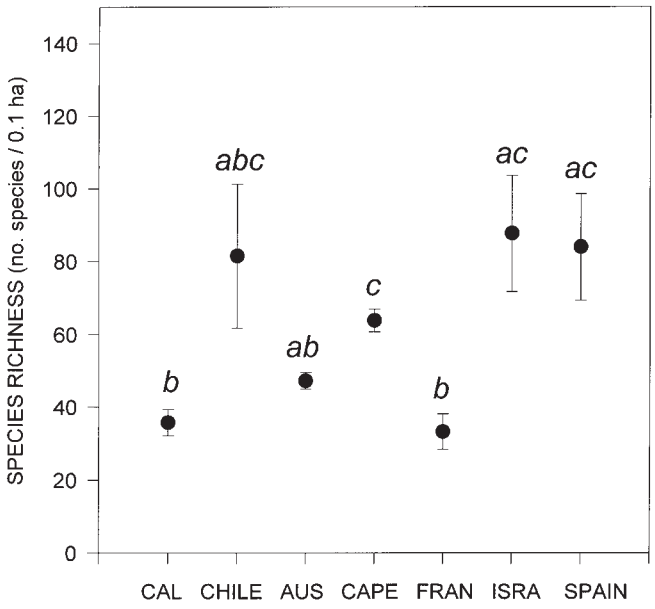

Figure 2. Species richness at the 0.1 ha scale (mean and SE bar) in regions with Mediterranean-type climate: California (CAL, $n = 14$), Chile (CHILE, $n = 4$), south-west Australia (AUS, $n = 97$), South African Cape region (CAPE, $n = 45$), north-west Mediterranean (FRAN, $n = 9$), east Mediterranean (ISRA, $n = 10$) and south-west Mediterranean (SPAIN, $N = 5$). Data from Westman (1988), Marañón (1985), and this study. Same letters indicate non-significant differences (at $P = 0.05$ level) after a *post-hoc* HSD Tukey's test for unequal sample sizes.

($n = 5$ and 9, respectively). On the other hand, Australia (97 plots) and South Africa (45 plots) are more adequately represented in the Mediterranean-wide database of species richness at the 0.1 ha scale.

Annual plant species contribute mostly (80–100 species) to the high species richness of grazed oak woodlands in the east (4 plots) and south-west (1 *dehesa* plot) Mediterranean regions. Richness of woody species, mostly shrubs, is relatively high (20–30 species/0.1 ha) in woodlands and shrublands of Chile, south-west and east Mediterranean.

All the results revised above concern vascular plants. Unfortunately, there is a lack of information about non-vascular plant diversity, at the 0.1 ha scale, and comparisons with other Mediterranean regions are thus not feasible.

Family diversity and species pool

Combining the four 0.1 ha sites of the Aljibe Mountains, we counted 60 woody species, belonging to 24 families. This same set of 24 plant families contained 233 woody species in the regional flora (Valdés et al. 1987). These families are unevenly distributed among community types (Table 3). When compared with the representation at the regional level, the higher abundance of Ericaceae in the heathland and *Q. suber* woodland is remarkable. On the other hand, woody Cistaceae, Fabaceae and Lamiaceae present a contribution to the plot woody species diversity similar to that in the woody flora of W. Andalusia (Table 3).

A similar analysis for the 124 spermatophyte herbaceous species present in the four plots showed that Asteraceae,Fabaceae and Poaceae were the most represented

Table 3. Family contribution to the community diversity.

Family	*Quercus canariensis* forest	*Quercus suber* woodland	Heathland	*Quercus coccifera* shrubland
Woody plants				
Cistaceae	1^{ns}	2^{ns}	5^{ns}	4^{ns}
Ericaceae	2^{ns}	5^{**}	5^{***}	3^{ns}
Fabaceae	4^{ns}	4^{ns}	4^{ns}	3^{ns}
Lamiaceae	1^{ns}	4^{ns}	3^{ns}	3^{ns}
Herbaceous plants				
Asteraceae	5^{ns}	9^{ns}	6^{ns}	3^{ns}
Fabaceae	0^{ns}	7^{ns}	1^{ns}	3^{ns}
Poaceae	8^{ns}	18^{***}	11^{***}	6^{ns}

Values are observed number of species of each family in the 0.1 ha plots. Superscript indicates significance levels in the comparison between observed number of species and expected from the woody and herbaceous regional species pool (Valdés et al. 1987). Significance of multiple equivalent tests for comparison of percentages is corrected by applying the Bonferroni technique (Rice 1989), considering all tests in each row as equivalent (ns = non-significant, $^{**}P < 0.01$, $^{***}P < 0.001$).

families. The comparison with the herbaceous species pool in W. Andalusian flora revealed that *Q. suber* woodland and heathland plots presented a significantly higher representation of Poaceae than expected (Table 3).

Woody plant communities and environmental factors

The floristic matrix of relative cover of 85 woody species in 44 sampling sites was analysed in combination with a set of 8 environmental variables for the same sites, by CCA analysis. The ordination of the sites, the types of woody communities (as defined by cluster analysis) and the main (significant) environmental factors are shown in Figure 3. The first axis explained 9.9% of variance and was significantly correlated with environmental variables ($P = 0.04$ for Monte Carlo test). It had negative correlation with altitude ($r = -0.53$, $P < 0.01$) and fire incidence ($r = -0.48$, $P < 0.01$), and positive with soil pH ($r = 0.71$, $P < 0.01$), browsing pressure ($r = 0.55$, $P < 0.01$) and overstorey tree cover ($r = 0.41$, $P < 0.01$). The second axis explained 8% of variance and was also correlated with environmental variables

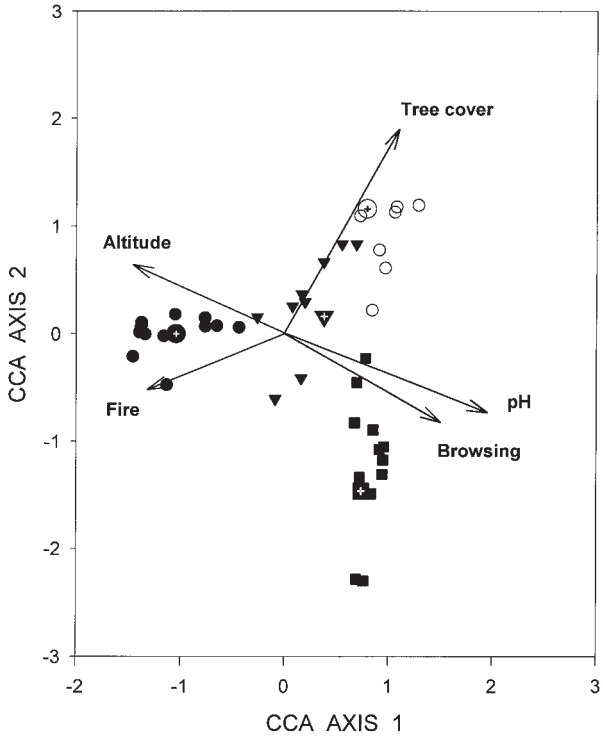

Figure 3. Ordination of shrub cover samples by CCA analysis. Symbols for community types are: (●) heathlands, (▼) *Quercus suber* woodlands, (○) *Q. canariensis* forests and (■) *Q. coccifera* shrublands. Enlarged symbols with cross inside indicate the permanent 0.1 ha plot in each vegetation type. Arrows mark the correlation with environmental factors (multiplied by 3 for clarity).

($P = 0.01$ for Monte Carlo test). It was significantly and positively correlated with overstorey tree cover ($r = 0.81$, $P < 0.01$) and negatively with soil pH ($r = -0.31$, $P < 0.05$) and browsing pressure ($r = -0.36$, $P < 0.05$).

The main ecological trend (indicated by axis 1) in woody species distribution and abundance was associated to a topographic and soil acidity gradient, ranging from open heathland on ridges, subjected to frequent burning, through evergreen *Q. suber* woodlands on slopes, at an intermediate stage, to semi-deciduous *Q. canariensis* woodlands on valley bottoms, which experience more fertile and humid conditions. All three of the woody communities are found on sandstone-derived soils.

A secondary ecological trend (indicated by axis 2) separated the *Q. coccifera* shrublands found on basic soils, at lower altitude sites and subjected to more browsing pressure, from the *Q. canariensis* woodlands found on acid, sandstone-derived soils, which had the highest overstorey tree cover. This general trend supports the pattern found in previous studies (Ojeda et al. 1995, 1996; Marañón et al. 1999).

Biodiversity components of the shrub layer

There were significant differences between communities for all the diversity parameters, except for equitability (Table 4 and Figure 5). The *Q. canariensis* woodland understorey, at the more mesic and fertile extreme of the gradient, had a moderate species richness, a low number of endemic taxa but the highest taxonomic singularity. The *Q. suber* woodland understorey, at intermediate stages in the gradient, had the highest species richness and (Shannon) diversity value, a moderate richness of endemics, and a moderate taxonomic singularity. The open heathland, at the more acidic, nutrient-poor, extreme of the gradient, had a moderate species richness and a low taxonomic singularity, but had the highest endemism level. The samples of *Q. coccifera* shrubland, on limestone, separated by a secondary axis associated with

Table 4. Mean values (±SD) of five diversity parameters of woody plant communities in the Aljibe Mountains.

	Quercus canariensis forest ($n = 13$)	*Quercus suber* woodland ($n = 10$)	Heathland ($n = 13$)	*Quercus coccifera* shrubland ($n = 8$)	F (3, 40)
Species richness	14.5 ± 2.8 a	19.6 ± 3.2 bc	15.5 ± 4.4 ab	19.0 ± 6.6 ab	4.50**
Shannon diversity	1.8 ± 0.4 a	2.2 ± 0.2 bc	1.9 ± 0.2 ab	1.8 ± 0.4 ab	3.89*
Equitability	0.66 ± 0.1 a	0.73 ± 0.04 a	0.71 ± 0.1 a	0.62 ± 0.1 a	2.94*
Endemic richness	1.8 ± 0.9 c	4.3 ± 1.8 b	7.2 ± 2.4 a	1.5 ± 1.2 c	34.40***
Taxonomic singularity	0.37 ± 0.12 a	0.18 ± 0.02 b	0.16 ± 0.02 c	0.42 ± 0.12 a	39.48***

ANOVA *F*-statistic values on rank-transformed data are indicated. Same letters within a row indicate non-significant differences between communities after HSD Tukey's tests. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

high calcium content in soil, had a moderate species richness and high taxonomic singularity but very few endemic species.

Biodiversity components of the herbaceous layer

Figure 4 represents the ordination diagram for the first two axes of the DCA analysis of 114 herbaceous species in 200 quadrats (50 × 4 sites). The first axis (eigenvalue = 0.751) ordered towards the positive end to the *Q. canariensis* understorey samples, with a set of characteristic species (having high scores) such as *Asplenium onopteris, Geranium purpureum, Scrophularia laevigata* and *Senecio lopezii*. At the opposite end, there was a mixed group of samples including open heathland and *Q. suber* understorey.

The second axis (eigenvalue = 0.485) separated towards the positive end, to the samples of *Q. coccifera* shrublands, associated with species (of high scores) such as *Aphyllantes monspeliensis, Hyparrhenia hirta, Stipa tenacissima* and *Galium boissieranum*. The third axis (eigenvalue = 0.310, not shown in the figure) separated the group of *Q. suber* understorey samples (mean score = 272, and SD = 32.5) from the open heathland samples (mean score = 146, and SD = 22.8).

The variation in the herbaceous layer, between the four community types, was significant for all the biodiversity components, except for the taxonomic singularity (Table 5). There was an overlapping rank in species richness within the three communities on sandstone: *Q. canariensis* understorey (the highest), *Q. suber* understorey (intermediate) and open heathland (the lowest), whereas the *Q. coccifera* shrubland

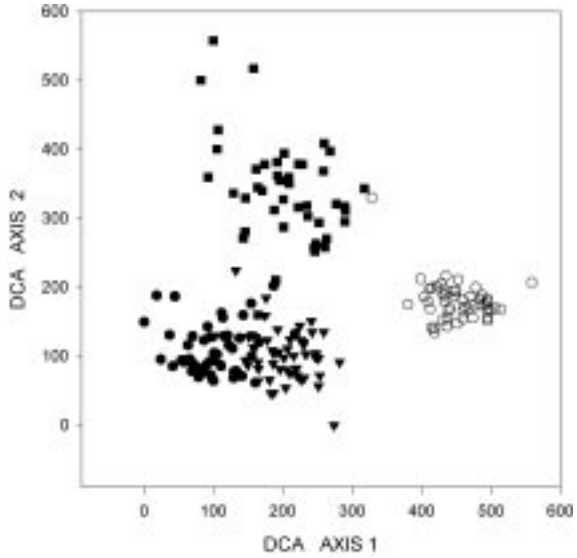

Figure 4. Ordination of herbaceous quadrat samples by DCA analysis. Symbols for community types as in Figure 3.

Table 5. Mean values (±SD) of biodiversity components of the herbaceous layer in four community types.

	Quercus canariensis forest ($n = 50$)	*Quercus suber* woodland ($n = 50$)	Heathland ($n = 50$)	*Quercus coccifera* shrubland ($n = 50$)	$F(3, 196)$
Species richness	8.6 ± 2.8 a	8.0 ± 3.0 ab	7.1 ± 2.4 b	3.5 ± 1.2 c	43.94***
Endemic richness	1.5 ± 0.8 b	0.9 ± 0.9 c	2.8 ± 1.0 a	0.5 ± 0.7 c	70.14***
Taxonomic singularity	0.33 ± 0.01	0.27 ± 0.01	0.29 ± 0.01	0.30 ± 0.03	1.78ns

ANOVA F and P values are indicated; same letters in a row mean a non-significant difference in the multiple comparison of the means after HSD Tukey's test. *** $P < 0.001$, ns = non-significant.

on limestone was much poorer in herbaceous species than all the sandstone sites (Figure 5).

There were 28 endemic herbaceous taxa in the 200 quadrats explored but they were unevenly distributed among plant communities. The highest density of herbaceous endemics was found in the open heathland (mean of 2.8 and maximum of 5 per 0.25 m^2), and the lowest in the *Q. coccifera* shrubland (mean of 0.5 per 0.25 m^2 quadrat; 64% had no endemics) (Table 5 and Figure 5).

Species-area relationship

The species-area relationships for Andalusia and the South African Cape Floristic Region (CFR hereafter) floras are shown in Table 6 and Figure 6. Despite the scarcity of data points, regressions were significant for both regions ($R^2 = 0.992$; $d.f. = 1, 4$; $P < 0.0001$ for Andalusia and $R^2 = 0.997$; $d.f. = 1, 2$; $P < 0.001$ for the CFR). The regression slope for the CFR was significantly ($F = 8.87$; $d.f. = 1, 6$; $P < 0.03$) steeper than that for Andalusia. At the 0.1 ha scale, Aljibe samples were somewhat richer in species than CFR plant communities (Figures 2 and 6). However, at a broader, regional scale (both Andalusia and the CFR regions cover about 90000 km^2) species number was much higher in the CFR (Figure 6).

Discussion

Community-level diversity

Despite the theoretical consideration of community level biodiversity in modern comprehensive treatments (UNEP 1995), few attempts at studying how biodiversity is organised in plant communities have been achieved (but see Cowling et al. 1992; Ojeda et al. 1995, 1996; Marañón et al. 1999). In this study, we supply data on several components of biodiversity in plant communities which support their high value for conservation assessment. Woodlands and shrublands of the Mediterranean Basin are

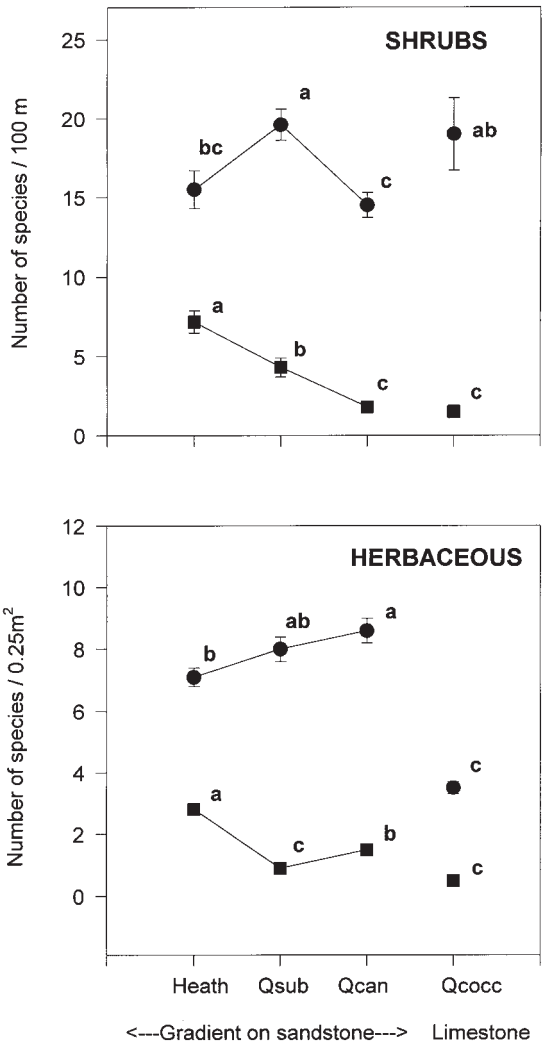

Figure 5. Variation across community-types in species richness (●) and number of endemic species (■), in both shrub and herbaceous layers. Community types are open heathlands (Heath), *Quercus suber* woodlands (Qsub) and *Q. canariensis* forests (Qcan) along the ecological gradient on sandstone, and the *Q. coccifera* shrubland (Qcocc) on limestone.

richer in plant species than neighbouring temperate communities in Europe (Naveh and Whittaker 1979; Grubb 1987). The geographical location of the Strait of Gibraltar and the peculiarity of its physical environment, with oceanic influence and dominance of sandstone-derived acid soils (edaphic islands in a basic-soil region) have probably contributed to the evolution of plant species diversity of heathlands and woodlands in the Aljibe Mountains (Arroyo and Marañón 1990; Ojeda et al. 1995). Considering our plots of *Q. coccifera* shrublands on limestone, marl and clay surrounding the

Table 6. Area sizes, species number and information sources for sites used in determining species-area relationships represented in Figure 6.

	Area size	Species number	Source
Andalusia (S. Spain)			
Quadrat ($n = 200$)	0.25 m^2	6.8*	This study
Plot ($n = 4$)	1000 m^2	69.5*	This study
Sierras de Algeciras	123 km^2	667	Gil et al. 1985
Algeciras region	2848 km^2	1174	Valdés et al.1987
Western Andalusia	45189 km^2	2332	Valdés et al.1987
Andalusia	87268 km^2	3500	B. Valdés (pers. comm.)
Cape Floristic Region (S. Africa)			
Quadrat ($n = 45$)	1 m^2	13.5*	Westman 1988
Plot ($n = 45$)	1000 m^2	60.3*	Westman 1988
Cape Peninsula	2250 km^2	2250	Cowling et al. 1992
Cape Floristic Region	90000 km^2	8500	Bond and Goldblatt 1984

* Average numbers.

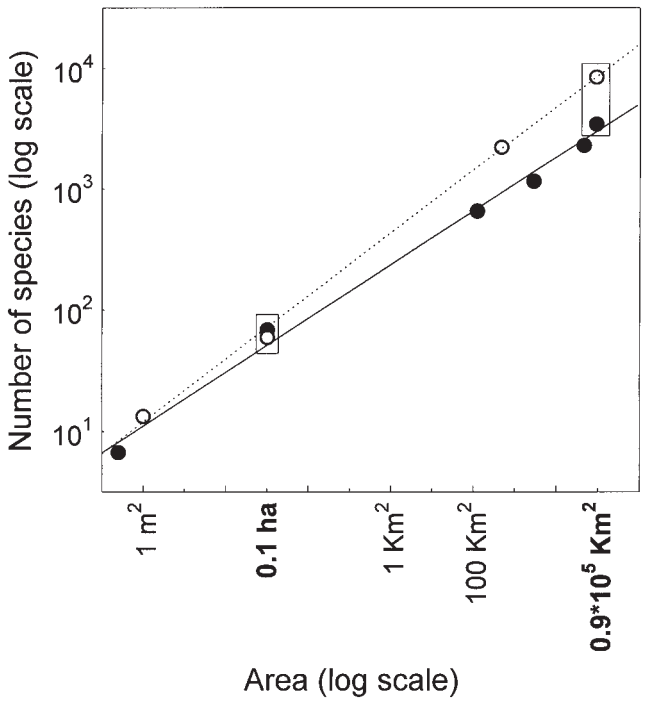

Figure 6. Relationship between plant species number and area for the Andalusian region in south Spain (filled circles and solid line), and for the Cape floristic region in South Africa (empty circles and dotted line). Compared data having equal area are enclosed in rectangles.

Aljibe, as a reference for a typical garrigue shrubland type, widespread in the West Mediterranean, we can state that Aljibean communities on sandstone have a similar species richness than the average Mediterranean shrubland in the shrub layer, but a higher endemic richness, especially the open heathlands on ridges. Regarding the herbaceous layer, the Aljibean woodlands and shrublands are richer in species number and also have more endemic taxa than the average garrigue shrubland.

At a world-Mediterranean scale, the diversity of vascular plant species (at the 0.1 ha scale) for the Aljibean evergreen woodland (95 species) is as high as for the most diverse communities, such as the heavily grazed woodlands in Israel (Cowling et al. 1996). Moreover, we should add more than 20 species of non-vascular plants (ferns, bryophytes and lichens), which are rarely included in the existing databases despite representing a significant contribution to plant diversity. Hernández-Gallego et al. (1998) have recently recorded 25 bark macrolichens in 0.1 ha plots of *Q. suber* (mean of 10.6, $n = 5$) and *Q. canariensis* woodlands (mean of 7.8, $n = 5$) in the study area.

The relatively high species diversity in the Aljibe Mountains contrasts with the reduced diversity in temperate European heathlands (Gimingham 1972). As a matter of fact, in the 22 heathland community types considered by Rodwell (1991) for Great Britain, the number of species (both vascular and non-vascular) per community sample ranged from 7 to 29 (mean of 17.6; non-vascular species averaging 42%). Considering all vascular species present in each community type, woody species (mean of 8.7) were fewer than herbaceous (mean of 26.0). Further south, close to the limit between boreal and Mediterranean regions in the Iberian Peninsula (where many species are shared with south Iberian, truly Mediterranean heathlands) woody species ranged from 7 to 20 and herbaceous from 6 to 18 (elaborated from Loidi et al. 1997). Although sampling areas were usually much lesser than 0.1 ha in the above mentioned studies, they were aimed to record all the species present in the communities, thus still giving some valuable comparative figures. Diversity levels of Aljibe heathlands are closer to those of South African mediterranean heathlands (i.e. fynbos) than to those of neighbour temperate European heathlands. The diversity pattern found at the community level in these heathlands is similar to the general pattern of diversity reported for *Erica* species at a continental, Euro-Mediterranean scale by Ojeda et al. (1998). The high representation of Ericaceae in the Aljibe open heathlands and *Q. suber* understoreys (many of them being indeed heathlands) is parallel to the diversity of these woody plant communities, and represents a floristic link with the highly species-rich fynbos flora of the South African CFR (Bond and Goldblatt 1984; Oliver 1989; Moll 1991).

Shrub and herbaceous layers

Different life-forms, such as trees, shrubs and herbs, have different diversity patterns (Grubb 1987). Within the environmental gradient on sandstone, we have found the highest diversity of woody species at intermediate stages, as expected if diversity is

limited by nutrient-deficiency at one end of the gradient, and by competition at the other end (Grime 1979; Rosenzweig and Abramsky 1993; Ojeda et al. 1995). However, the diversity of herbaceous species increased slightly towards the more fertile end of the gradient, that is, in the *Q. canariensis* woodland understorey, probably benefiting from the semi-deciduous nature of the tree overstorey. A functional analysis of the species composing this community, e.g. relative importance of woodland ephemerals, is needed to fully understand this pattern of diversity.

Comparatively, the species richness of the garrigue-like *Q. coccifera* shrubland, although relatively high for woody species, is very low for non-woody ones. This community is also poor in non-vascular species, especially when compared with the nearby woodlands and heathlands on sandstone (Table 2). The drier soil conditions of this habitat would reduce the diversity of ferns, bryophytes and algae, and the basic substrate is low suitable for epilithic lichens (Ozenda and Clauzade 1970).

Open heathlands on ridges have the highest density of endemic taxa in both the woody and the herbaceous layers. The peculiarity of the soil condition (nutrient-poor and acidic), in a limestone-dominated Mediterranean Basin, has probably favoured this extraordinary accumulation of taxa with a narrow distribution. This had been already ascertained for woody plants (Ojeda et al. 1995, 1996) and it is extended here to herbaceous plants (most of them being perennials in heathlands). These endemics have been most probably preserved from extinction because of the low fertility of the soils they grow on, not suitable for crop nor forage production. However, they are currently threatened by the expansion of the subsidised tree plantations in marginal, low-productive lands. These endemic-rich heathlands should be fully surveyed, mapped and protected as reserves for plant diversity.

The shrubby understorey of the semi-deciduous *Q. canariensis* woodlands is relatively poor in endemic taxa, although one of them, *Rhododendron ponticum* subsp. *baeticum* has been included in the regional red list as a 'extinction-risk species' and is legally protected. At the herbaceous layer, there is a relatively high amount of endemic taxa in the *Q. canariensis* woodland understorey, most of them being also perennials. The biology of this group of woodland herbs, such as *Arisarum proboscideum* and *Senecio lopezii*, which have sought refuge in moister microclimate habitats within the Mediterranean, has been poorly studied. They might be used as indicators of the 'good health' of woodland conditions. They are currently threatened though by the extensive and subsidised 'cleaning' practices which tend to convert the complex, multilayered woodlands in thinned, pruned, light-exposed tree stands, therefore favouring the replacement of these specialist woodland understorey herbs by widespread, generalist, light-demanding species.

A high density of singular woody species (those belonging to low-diversified genera), is found in the *Q. canariensis* woodland understorey. The moister and shadier conditions have probably acted as a refuge for pre-Glaciation, relict taxa, being modern, truly Mediterranean taxa, belonging to high-diversified genera (and thus less singular), less able to colonise those habitats. However, this pattern is not found alto-

gether at the herbaceous layer, in which there are no significant differences along the gradient. A faster differentiation of modern, Mediterranean herbs than their woody counterparts (Raven 1973), would have made possible for them to colonise these habitats and grow under the relict, pre-Mediterranean shrubs and vines.

Spatial patterns and regional diversity

Regional diversity is the product of local diversities and differentiation diversity in relation to environmental heterogeneity (Cowling et al. 1992, 1996). The high local diversity is partly determined by the low rates of competitive displacement that result from low soil nutrients and summer drought, coupled with a moderate intensity of disturbance by fire and grazing (Huston 1994). The second factor, differentiation diversity, is determined by the evolutionary turnover of habitat specialists and geographical vicariants in a heterogeneous landscape.

At the 0.1 ha scale, Aljibe Mountains communities were slightly more diverse than those from the CFR. However, the steeper regression slope for the CFR in the species-area comparative study (Figure 6) is a reflection of its higher differential diversity and regional richness, when compared with Andalusia or any other Mediterranean-type area (Cowling et al. 1992).

It is worth noting that the European Mediterranean area (Andalusia) included in the species-area regression analysis presents a high diversity of vegetation types (e.g., sclerophyllous forest, high mountain cushion-like scrubland, lowland macchia and garrigue), with Mediterranean heathlands being relatively scarce. This latter vegetation type is widespread in CFR (Moll 1991; Cowling and Holmes 1992), and is physiognomically more homogeneous there. Therefore, this analysis highlights firstly the well-known regional diversity of the CFR flora and secondly the less known high local diversity within communities in the Aljibe Mountains. Additional comparative work is needed in order to elucidate whether evolutionary forces, such as fire and soil nutrients, proposed as floristic diversity drivers in CFR (Linder 1985; Cowling 1987) are also responsible for the high diversity in Aljibean heathlands.

A plant diversity hot spot

The high community diversity is paralleled by a high floristic diversity. Most of the literature on biodiversity hotspots focuses on a regional scale, with emphasis on different spatial levels. In the case of plant diversity, it deals mainly with floras (WWF and IUCN 1994). At the regional level, there is some evidence supporting the status of a plant diversity hot spot for the Aljibe Mountains, within the context of European and world-Mediterranean regions. In a regional analysis of the Mediterranean Basin, Médail and Quézel (1997) classified the Baetic-Rifan complex as a hotspot for plant diversity. This was based on evidence of species richness (about 3500 species in total) and endemism (greater than 50% in Sierra Nevada), and excluded the Aljibe Moun-

tains. In addition to a marked geologic and climatic heterogeneity, the great diversity of substrata, such as serpentine, dolomites and gypsum (common in the Baetic range) were claimed by these authors to account for the high biodiversity. However, they did not mention the acid, sandstone-derived soils, to which most endemic taxa are associated in the Strait of Gibraltar area (Ojeda et al. 1996; Arroyo 1997).

Other treatments (WWF and IUCN 1994) considered the whole Baetic range, including the Aljibe Mountains (here named Algeciras Mountains), as a centre of plant diversity (the 'Baetic and Sub-Baetic Mountains Centre') at a world-wide scale (but excluded the southern, Moroccan part). According to this latter study, the main contribution to biodiversity of the Aljibe Mountains is given by the disjunct Macaronesian and temperate elements, whereas the high richness of edaphic endemism is overlooked. These endemic taxa have features not typical of most endemics in the Baetic centre, such as neat taxonomic distinctness and shrubby life-form, apparently associated with edaphic speciation without orographic isolation (Arroyo 1997).

In general, regional treatments consider only species and endemic richness as parameters for biodiversity. However, there is a theoretical framework to deal with other parameters, such as character richness as a surrogate from taxonomic classification or spatial turnover of species for quantifying the biodiversity in a region (Vane-Wright et al. 1991; Williams et al. 1991). At the Iberian Peninsula scale, Castro et al. (1996) employed this type of approach, based on the distribution of 2133 taxa (plant species and subspecies) in 50×50 km map grids and 801 taxa (10% of the flora) in 10×10 km map grids. Many grids (4–7) included in the Baetic range are placed among the top ten of plant diversity in the Iberian Peninsula. The most remarkable result of this study (in our context) is the high biodiversity value applicable to the 'Sierra de Algeciras' (equivalent to Aljibe Mountains): it ranked third to fourth when endemism weight or character richness was considered (and second within the Baetic region, after the high elevation Sierra Nevada). This approach stresses the regional importance of the plant diversity of Aljibe (or Algeciras) Mountains in comparison with former and more traditional treatments. Therefore, the Baetic-Rifan hotspot of plant diversity should explicitly include the whole Strait of Gibraltar area and, particularly, the Aljibe Mountains.

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